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1 Soil aggregation, ecosystem engineers and the C cycle

2

3 Patrick Lavelle¹, Alister Spain², Steven Fonte³, Jose Camilo Bedano⁴, Eric Blanchart⁵, Victor

4 Galindo⁶, Michel Grimaldi⁷, Juan Jose Jimenez⁸, Elena Velasquez⁹, Anne Zangerlé¹⁰

5 1. Université Paris Sorbonne, IEES-BIODIS, Paris, France

6 2. The University of Western Australia, Perth, Australia

7 3. Colorado State University, Fort Collins, USA

8 4. National University of Río Cuarto, Córdoba, Argentina

9 5. IRD, UMR Eco&Sols, Montpellier, France

10 6. Universidad del Valle, Cali, Colombia

11 7. Centre IRD, IEES, Centre IRD, Bondy, France

12 8. Instituto Pirenaico de Ecología-CSIC, Jaca, Huesca, Spain

13 9. Universidad Nacional de Colombia, Palmira, Colombia

14 10. Ministry of Agriculture, Viticulture and Rural Development. ASTA, Luxemburg

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32 HIGHLIGHTS

33

34 1. Invertebrates and roots are essential drivers of soil aggregation, but often overlooked.

35

36 2. Manual separation and NIR spectroscopy allow classifying macro-aggregates according
37 to the physical or biogenic agents that produced them.

38

39 3. A simple field method is proposed to measure in situ rates of production and losses in
40 the different macro-aggregate pools.

41

42 4. Stocks, inputs and losses of C in aggregate pools characterize their contribution to C
43 cycling and conservation.

44

45 5. This simple and robust approach can support the identification of management
46 practices that best store and conserve C in soils

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50

51 **Abstract:** Soil aggregation and its effects on soil C storage have been addressed in
52 thousands of research articles over the last 40 years. Research has been mostly focussed
53 on the resistance of aggregates to mechanical disruption and the role of organic matter in
54 aggregate stabilization. On the other hand, relatively little attention has been paid to
55 identifying the microbial, plant root and macro-invertebrate actors and physical processes
56 that continuously create and destroy aggregates. The sum and dynamics of these
57 processes determines the ability of soils to store and conserve C. Understanding the
58 interactions between aggregation dynamics and C transformations in soils therefore
59 requires a precise identification of the agents that produced aggregates and knowledge of
60 the rates of formation and persistence in the pools thus identified.

61 We propose to separate macro-aggregated components of different, physicogenic and
62 biogenic origins from non-macro-aggregated soil on a morphological basis, using a simple
63 visual technique. The specific biological or physico-chemical agent which produced each
64 individual macro-aggregate can then be determined using Near Infrared Spectrometry
65 (NIRS). A general description of the distribution and quality of organic matter among the

66 different groups of macro-aggregates can be made. Simple soil re-aggregation or dis-
67 aggregation test conducted in field conditions further measure the production of different
68 macro-aggregates with time and their mean residence times in the studied soil.
69 Respirometry measurements on each recognized category of macro-aggregates evaluate
70 the respective C losses through respiration. The methods described here will allow the
71 dominant pathways of C flow at a given site to be characterized and possible management
72 options to increase C storage identified. We finally discuss the different assumptions made
73 to build this simple model and offer ways to test the methodology under field conditions.

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76

77 1. Introduction

78

79 While improved soil management offers one of many promising approaches for climate
80 change mitigation, soil scientists and technicians are increasingly faced with the challenge
81 of proposing and testing viable strategies to enhance C sequestration in soils (Altieri et al.,
82 2015; Poeplau and Don, 2015; Paustian et al., 2016; Powlson et al., 2016; Smith et al., 2016;
83 Bedano et al., 2019). As a major C reservoir, soil organic matter on Earth is estimated to be
84 1500 to 2400 Gt C, that is more than twice the mass of the C contained in the atmosphere
85 (860 Gt). In addition, soils currently sequester an additional 3.2 ± 0.7 Gt C annually,
86 equivalent to 29.4% of the annual emissions from fossil fuel burning. However, this positive
87 contribution is offset each year by 1.5 ± 0.7 Gt C emitted as a consequence of land use
88 change and soil degradation (Le Quéré et al. 2018). We currently do not know whether
89 soils will continue to store C as climate change accelerates, or lose it -as land degradation
90 continues- and this represents a major uncertainty for climate change projections
91 (Carvalhais et al. 2014). The international 4 per 1000 initiative proposes offsetting
92 anthropogenic emissions by storing every year an extra 0.4 % in agricultural soils through
93 adequate management options (Minasny et al., 2017). Such a challenge will require precise
94 tools for implementation and monitoring at plot and farm scales. We argue that our

95 understanding of the mechanisms involved in the stabilization of C in soils and ways to
96 harness our knowledge under field conditions need to be improved.

97

98 The Importance of physical protection for organic matter conservation

99 Three processes allow organic matter conservation in soils: physical protection in
100 aggregated structures, the association of transformed organic matter to mineral particles in
101 organo-mineral complexes and chemical recalcitrance (Six et al., 2004). We argue that
102 these processes are not independent and soil aggregation is expected to be a key process
103 in facilitating all three (Amezketta, 1999; Sollins et al., 1996; Feller and Beare, 1997; Six et
104 al., 2000a, 2002a and b; 2004; Von Lutzow et al., 2006). Physical protection is likely a first
105 step in conservation, that slows down the mineralization process by isolation of microbes
106 from their organic substrates and/or limits water and oxygen supplies; Kuzyakov et al.,
107 2015; Negassa et al., 2015; Keiluweit et al., 2016). Suitable conditions are then created for
108 the other two processes to occur and a great part of SOM storage in soils may be in the
109 form of organo-mineral complexes (Cotrufo et al., 2019). Organic matter accumulation has
110 positive feed backs on in turn is widely acknowledged as an essential component for
111 aggregate formation and stabilization (Amezketta, 1999; Six et al., 2004; Abiven et al, 2009;
112 Fultz et al., 2013; Gumus and Seker, 2015; Zhu et al., 2017).

113 However, a variable proportion of the leaf and root litter Carbon may have been
114 mineralized before these complexes are formed. It depends on the suite of initial
115 decomposition processes that associate physical processes like comminution, transfers in
116 the soil profile, inclusion in aggregate structures and chemical transformations associated
117 to digestion and humification (Lavelle and Spain, 2001). In determined conditions of
118 climate, soil and plant cover, the stabilization of C in soils, in particulate (POM) or mineral
119 associated (MAOM) forms thus depends to a great extent on the efficiency of physical
120 protection of organic matter against decay at macro- or microsite scales (Parton et al.,
121 1988, Lavelle, 2002; Jimenez and Lal., 2006; Kuzyakov et al., 2015).

122 The long admitted alternative option for accumulation in soils of C pools made recalcitrant
123 because of their chemical compositions is now strongly challenged (Lehmann et al., 2015).

124 Priming effects triggered by water-soluble organic compounds migrating down the soil
125 profile or released by roots and invertebrate soil ecosystem engineers actually allow the
126 mineralization of substrates reputed to be highly recalcitrant (Martin et al., 1992; Trigo et
127 al., 1999; Fontaine et al., 2007; Lehmann et al., 2015).

128 There is a relative dearth of knowledge, however, of the diversity of ways aggregates are
129 formed and the consequences this has on the amounts and quality of C concentrated and
130 conserved inside these structures.

131

132 What are soil aggregates??

133 Aggregates defined as “soil specific entities built from mineral and organic compounds with
134 stronger bonds between building blocks than with neighbouring particles”.....“have a size,
135 form and stability that is typical for individual soils depending on parent material and
136 texture, climate and vegetation, biological activity and management” (Yudina and
137 Kuzyakov, 2018). Their classification and evaluation are still largely determined by the
138 method used to view or isolate them.

139 Non-destructive viewing techniques require rather sophisticated approaches such as
140 tomography or the realization and image analysis of soil thin sections (Tracy et al., 2015;
141 Wang et al., 2016; Zhao et al., 2017; Scarciglia and Barca, 2017; Gutierrez-Castorena et al.,
142 2018). Isolating techniques separate aggregates according to their resistance to physical
143 rupture following dry or wet sieving or slaking in water or other liquid substrates (Elliott,
144 1986; Le Bissonnais, 1996). Isolating may provide different results from viewing techniques
145 since the energy used to isolate may determine the size of elements separated (Ashman et
146 al., 2003; Kravchenko et al., 2018).

147 Separation of macroaggregates according to their morphology is a simple method that
148 associates viewing and isolating approaches (Topoliantz et al., 2000; Velasquez et al.,
149 2007a). The major advantage is that it does not require sophisticated equipment and thus
150 can be applied by non-scientific operators, school children, students, technicians and
151 farmers to discover and quantify soil macro-aggregation.

152

153 Importance and diversity of macro-aggregates in natural soils

154 A wide range of possible mechanisms for aggregate formation exists, from the close
155 association of mineral and/or organic particles in microaggregates, at microsite scales of a
156 few tens of microns, to the production of highly organized long-lasting macro-aggregates
157 made by soil ecosystem engineers such as ants, termites and earthworms (Lavelle et al.,
158 1997; Tötsche et al., 2018, Zanella et al., 2018; Yudina and Kuzyakov, 2019). Aggregates
159 frequently have a hierarchical organization and it is widely thought that microaggregates of
160 a size < 250 μm , the most stable elements, are formed inside macroaggregates as part of
161 their stabilization process (Six et al., 2014).

162 Many types of macro-aggregates of physicogenic or biogenic origin can be distinguished
163 (Velasquez et al., 2007a; Zanella et al., 2018; Yudina and Kuzyakov, 2019). The simple visual
164 separation of biogenic aggregates produced by roots and macroinvertebrate shows their
165 importance in surface soil horizons: in natural soils of temperate (Pulleman et al., 2004) or
166 tropical regions (Velasquez and Lavelle, 2019; Grimaldi et al., 2014), aggregates of biogenic
167 origin, mainly produced by earthworm activities often represent 40 to 60% of the soil
168 weight in the upper 15 cm of soil.

169

170 Energy cost of forming aggregates

171 When considering the effects of soil aggregation on the C cycle, the release of C by
172 respiratory activities during their construction is often overlooked. It may be an important
173 element to consider when designing management options aimed at storing C in soils. For
174 example, populations of the earthworm *Reginaldia omodeoi* in savannas of Ivory Coast
175 ingest every year an estimated 850 Mg eq. dry soil and transform it into casts that are
176 compact and highly resistant macroaggregates with a rather complex general structure
177 (Lavelle, 1978; Blanchart, 1993; Blanchart et al., 1997). The mechanical work required to
178 burrow, ingest soil particles, take them through the gut and release them as casts is
179 allowed by the assimilation of 9% of the C contained in the ingested soil, that is 1.2 Mg C
180 $\text{ha}^{-1}\text{yr}^{-1}$ emitted as CO_2 through earthworm respiration (Lavelle, 1978). Energy cost derived

181 from C mineralization is expected to be lower for macro-aggregates formed by fungal
182 entanglement of particles since hyphae likely grow in the connected porous space of the
183 soil and do not spend energy moving particles. Data to address this point however, are
184 lacking. The creation of physicogenic aggregates by processes like wetting/drying or
185 freeze/thaw alternances apparently has no direct C cost.

186

187 Temporal stability and turnover time of aggregates

188 Aggregates experience dynamic processes of creation, stabilization, ageing, destabilization
189 and disruption (Marquez et al., 2019). A precise description of their spatio-temporal
190 dynamics and turnover is therefore an obligate step in evaluating the effect of aggregation
191 on C storage and conservation in soils. Assuming that C mineralization is either decreased
192 or stopped in aggregated structures, we need to know how much C is protected in these
193 structures, to what extent, in which forms and for how long time.

194 We actually know little of the temporal stability of aggregates of different origins and thus
195 how long these structures will conserve C before they collapse. Macro-aggregates formed
196 by entanglement of soil particles, by fine roots or mycorrhizal and other fungal hyphae,
197 generally have rather short life times, from a few days to a few months (Plante and Mc Gill,
198 2002 ; De Gryze et al., 2005, Segoli et al., 2013); they tend to disaggregate when the fungal
199 hyphae or root disappear and/or organic binding agents are mineralized. On the other
200 hand, casts of the African endogeic species *Reginaldia omodeoi* can remain intact for long
201 periods of time – from 20 to 28 months - depending on soil texture and activity of
202 decompacting earthworm populations that feed on these structures and disperse them
203 (Blanchart et al., 1993b). Stabilized macro-aggregates are actually estimated to last up to
204 10 or 20 years if no disturbed (Lobe et al., 2011, Koesters et al., 2013; Marquez et al.,
205 2019).

206 Many studies have monitored the build-up or decrease of aggregation as a result of
207 experimental conditions or changes in management options (Beare et al, 1994; Bronick et
208 al., 2005; Calonego and Rosolem, 2008). However, the direct measurement of aggregate
209 turnover under steady state conditions is difficult. It has only been achieved, to our

210 knowledge, using labelling with very specific rare earth or isotopic tracers (Plante and Mc
211 Gill., 2002; De Gryze et al., 2005), tomography (Roose et al., 2016) or by using rather
212 complex mechanistic simulation models (Lavelle and Meyer, 1983, Martin and Lavelle,
213 1992; Segoli et al., 2013; Marquez et al., 2019). These approaches can help with
214 understanding aggregate turnover dynamics, but also have a number of limitations.

215

216 A field-based conceptual model and methodological approach

217 The rarity and diversity of attempts to describe aggregate life histories and dynamics is a
218 clear indication that the problem is complex. Actually, no simple conceptual or
219 methodological approach have been proposed so far. While much is known on the
220 aggregation process, its diversity and importance, we argue that a few critical elements are
221 still lacking to allow us to evaluate and accurately model the effect of soil aggregation
222 dynamics on C conservation. This exists as a serious impediment to identify management
223 practices and accurately predict their potential effect on soil C sequestration in a context of
224 climate change.

225 This paper starts with a general bibliometric analysis. The aim was to identify knowledge
226 gaps, that impede the implementation of a dynamic modelling of the soil aggregation
227 process and its effect on C conservation in soils. The lack of consideration of the role of soil
228 ecosystem engineers in general soil processes, is one such possible gap indicated by several
229 authors (Lavelle, 2000; Bottinelli et al., 2015; Filser et al., 2016; Jouquet et al., 2016). We
230 then propose a simple conceptual model where the conservation of C in soil depends on its
231 protection into macro-aggregates.

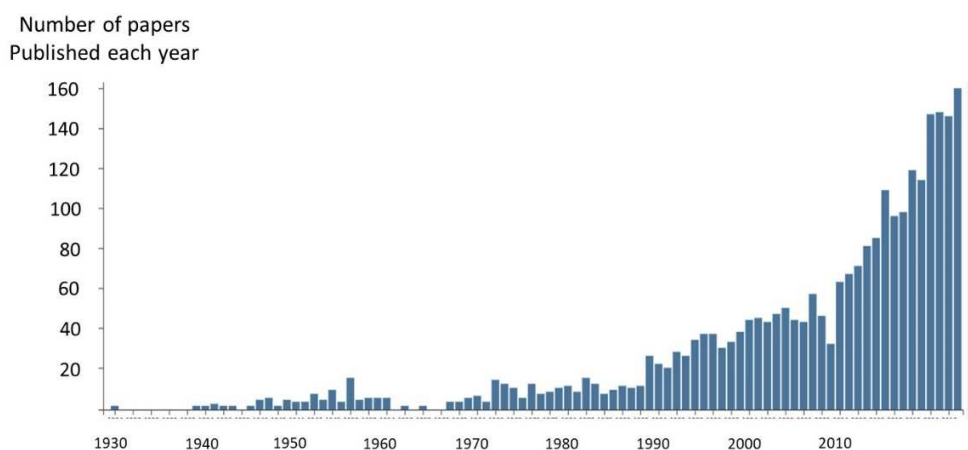
232 We finally discuss the coherence and feasibility of this approach in view of the assumptions
233 made and identify research needs to improve it. Particular emphasis is set on providing
234 concepts and methodologies accessible to non-specialized scientists, farmers and
235 technicians.

236

237 [2. Soil aggregation in the scientific literature](#)

238

239 A search of the ISI Web of knowledge in November 2019, with the words 'soil 'and
 240 'aggregat*' in title provided 2,692 papers, with a clear exponential increase occurring in the
 241 rates of publication on these and related topics over recent years. With the same keywords
 242 in topic, we obtained 77,427 articles. The large number of citations (>77,000), further
 243 illustrates the enormous interest in, and the importance of, this topic.



244

245 *Figure 1: Number of papers published each year with words "soil" and "aggregate*" in title*
 246 *(source ISI Web) from 1900 to present.*

247

248 The frequency of associated words in titles showed the major themes studied. **Organic**
 249 **matter** or **Carbon** was the most important topic associated with soil aggregates, treated in
 250 757 (28.1%) papers. This shows the strong association perceived between the aggregation
 251 process and soil organic matter cycling. **Stability** was the second topic in importance (572
 252 occurrences, 21.2%), a very important attribute of aggregates that measures their
 253 resistance to breakdown by physical stress, especially by water (301; 11.1%). **Soil**
 254 **management** (or till* or crop*) considered in 430 papers (16%) reflects the ongoing
 255 concern for physical degradation in managed soils and interest to identify options for
 256 reverting degradation. **Aggregate size** (418; 15.5%) is an important morphological attribute,
 257 considered an indicator of aggregate stability. **Water and erosion** (358; 6.7%) and **texture**
 258 (clay or text* or sand) (198; 7.4%) are studied for their important role in aggregate
 259 stabilization. In comparison, biological actors of aggregation comprised a low proportion of
 260 the papers. **Microbial** relationships with aggregation (microb* or microor* or bact* or

261 fung* or mycor*) were studied in only 307 (11.4%) papers, soil **macroinvertebrates**
262 (earthworm* or lumbric* or termit* or ant* or formic* or macroinvert*) in 56 papers (2%),
263 the same as **roots** (55; 2%). Finally, **turnover** of aggregates (7) or of organic matter in
264 aggregates (9) have been very little considered in aggregate research.

265

266 3. An alternative approach to assess aggregate-associated C dynamics

267

268 In their seminal paper, Tisdall and Oades (1982) proposed a comprehensive conceptual
269 framework to explain the origin, stabilization and dynamics of soil aggregation. They listed a
270 number of key features that characterize the physical organization of aggregated structures
271 and a diversity of mechanisms that provide stability against disruption. Such elements have
272 been thoroughly described and discussed in later reviews (Elliott, 1986; Feller and Beare,
273 1997; Six et al., 2002a, 2014; Tötsche et al., 2018) and different elements have been
274 introduced in recent modelling attempts (De Gryze et al., 2001, Marquez et al., 2019).
275 Although this model has inspired a large number of studies, measuring the different
276 compartments is still difficult and often requires rather high levels of expertise and
277 equipment. Modelling the ageing and disruption dynamics of aggregates is even more
278 difficult, partly because of the initial diversity of aggregate composition and structures that
279 has not been considered so far in monitoring and modelling attempts. Stabilization or de-
280 stabilization dynamics further depend on chemical, physical and biological processes
281 associated with local soil conditions and the quality and quantity of organic material
282 present in the aggregate.

283

284 3.1. General conceptual model

285

286 Our conceptual model is based on three simple assumptions:

- 287 1. Aggregate fractions should be separated according to their origin. This will prevent
288 the mixing of very different aggregates into a single category based solely on their
289 resistance to physical stress. We will recognize various pools of physicogenic or
290 biogenic aggregates of root or invertebrate origin (Topoliantz et al., 2000; Velasquez
291 et al., 2007a; Zanella et al., 2018). We expect each pool to have different dynamics

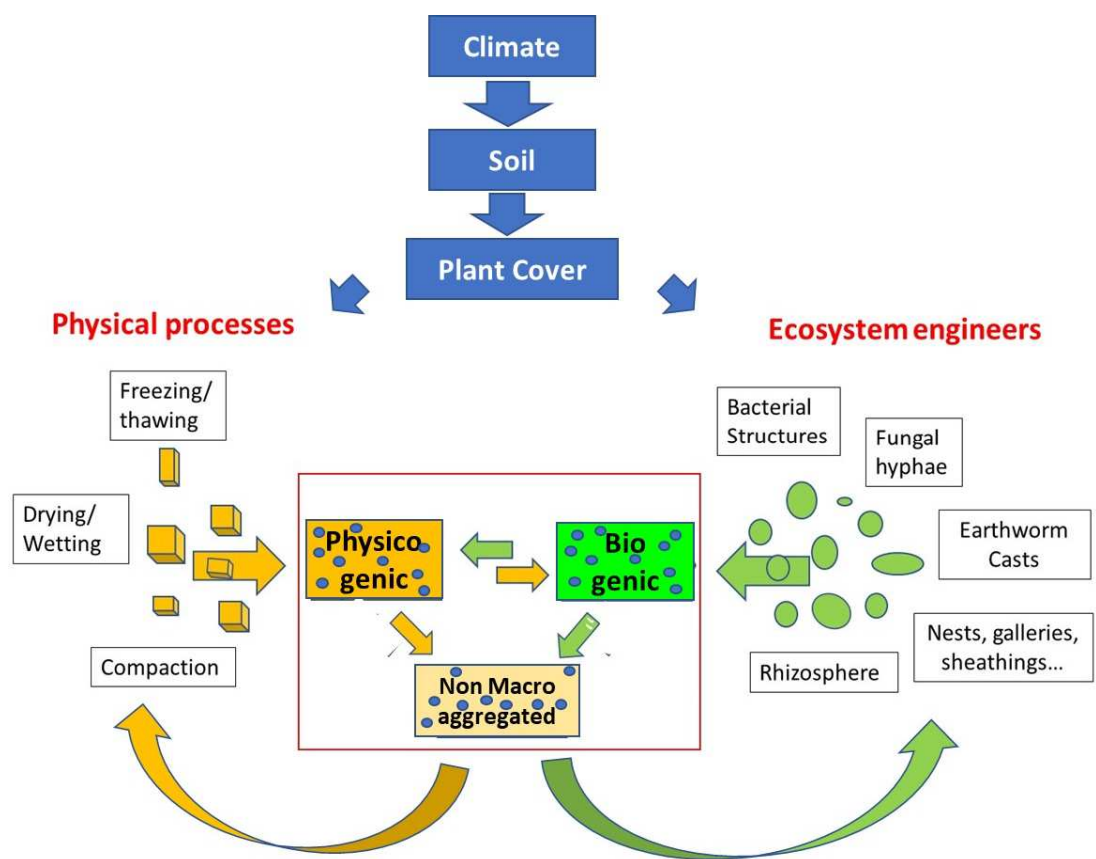
292 according to their initial diversity of compositions and structures (Hedde et al.,
293 2005).

294 2. Microaggregates are mainly formed within macroaggregates (Six et al., 2004) and
295 their dynamics are likely associated with the one of the larger structures that hosts
296 them. We expect, however, that disaggregation of macro-aggregated structures will
297 not go along with disaggregation of microaggregates and a pool of free
298 microaggregates may be comprised in the non-macro-aggregated soil fraction
299 (Tötsche et al., 2018).

300 3. Organic matter transformations are closely linked with aggregate dynamics. The
301 incorporation of organic matter to the soil matrix is mostly a biological process
302 associated with root growth, rhizodeposition, comminution, feeding and
303 bioturbation processes. Flux of water-soluble organic matter that may transit
304 through the porous space of the soil is expected to be negligible (Lavelle and Spain,
305 2001; Jimenez et al., 2006). Organic matter is present in different forms and
306 quantities in the different aggregated and non-macro-aggregated pools and
307 associated to specific mineral components and porous spaces (Daniel et al., 1997;
308 Capowiez et al., 2011; Arai et al., 2019). Mineralization rates are therefore likely
309 determined by conditions that occur in aggregates.

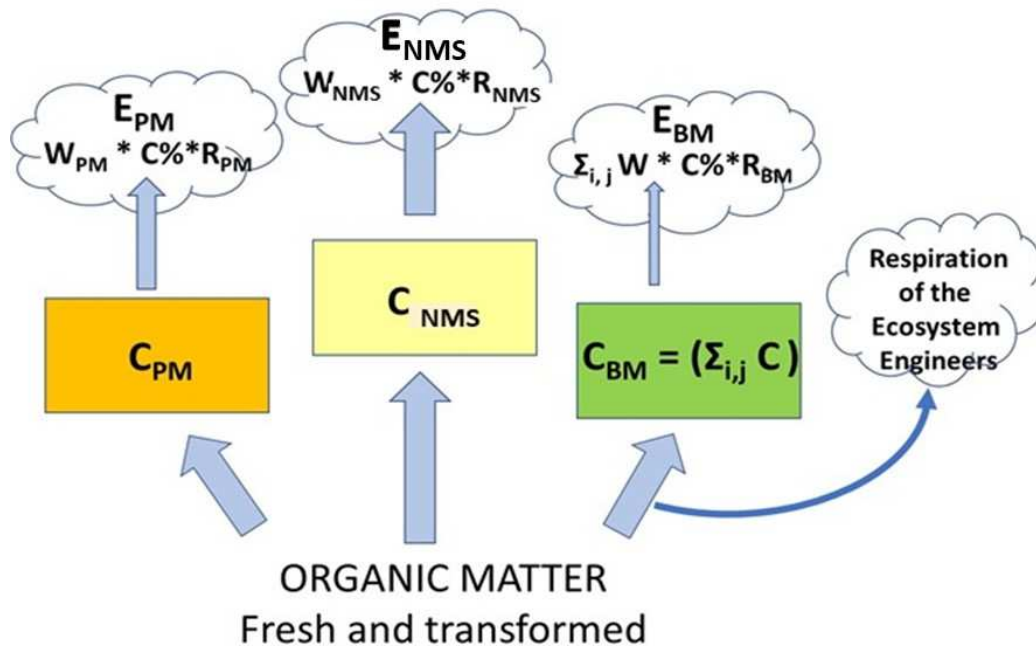
310 In a given set of environmental - climate, soil and plant cover- conditions, macro-
311 aggregates created by different processes and actors (see Fig. 2) accumulate in three
312 compartments, which have different turnover times and mineralization rates and
313 differently affect the overall C dynamics (Fig. 3).

314



315

316 *Figure 2: Conceptual framework for the diagnosis of soil macro-aggregation status and*
 317 *dynamics. Small circles in each category box symbolize microaggregates. Macroaggregates*
 318 *are classified in 3 categories, each of them having a definite number of sub categories*
 319 *indicated in boxes. Their dynamics involves creation from other aggregate pools, ageing and*
 320 *disruption that transfers their material to the non-macroaggregated pool, or a direct*
 321 *transformation into biogenic macroaggregates from the other 2 pools.*
 322



323

324 Figure 3: Flow of organic matter and gas emissions through the aggregated and non-macro-
 325 aggregated soil compartments.

326

327 *Carbon in physical macro-aggregates (C_{PM}), non-macro-aggregated soil (C_{NMS}) and biogenic*
 328 *macro-aggregates (C_{BM}).*

329 *E_{PM} , E_{NMS} and E_{CBM} are gases released by respiratory activities from the C_{PM} , C_{NMS} and C_{BM}*
 330 *pools respectively. W : respective weights of the C_{PM} , C_{NMS} and C_{BM} pools; $C\%$: % carbon*
 331 *contained in the respective pools; R_{PM} , R_{NMS} and R_{BM} : emission rate in %C of the different*
 332 *pools. Note that respiration of soil ecosystem engineers when they produce biogenic*
 333 *aggregates is an additional source of gas emissions.*

334

335 Three major steps are necessary to run this general model of soil aggregation and
 336 associated C dynamics (Figure 2 and 3).

337

- Diagnosis of the aggregation status of the soil that considers the origins and relative amounts of the different types of aggregates (Fig.2);

338

339

- Assessing the production and turnover of aggregates by measuring the flows of materials among the different aggregated and non-aggregated fractions (Fig 2);

340

341

- C cycling and aggregate dynamics: an analysis of the quality and quantity of C pools contained within each macro-aggregate or non-macro-aggregated fraction, their mineralization rates in the respective pools and the C losses and gains associated with their production, stabilization, ageing and disruption cycles (Fig 3).

342

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345

346 *3.2 Diagnosis of aggregation status*

347

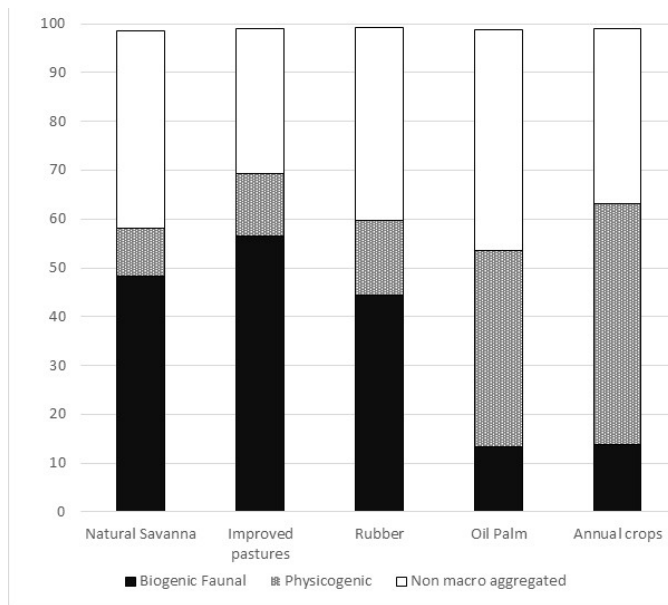
348 Separation and identification of the origins of aggregates is the first step in our approach.

349

350 Large macro-aggregated compartments

351 **Size limits.** There is a general agreement that a 250 μm size separates macro- from
352 microaggregates. Since it was first proposed by Tisdall and Oades (1982), this limit has
353 dominated the research although sub categories have been proposed within each class.
354 This paper focuses on the large macroaggregates > 2 mm sub category that can be easily
355 separated and identified.

356 **Origin and identity.** Manual fractionation allows the separation of soil into three main
357 fractions (non-macro-aggregated, physicogenic and biogenic macro-aggregates) based on
358 their sizes and general morphologies (Topoliantz et al., 2000; Pulleman et al., 2005;
359 Velasquez et al., 2007a). This method has been applied successfully to describe macro-
360 aggregation in a wide range of soils, with sandy to clayey textures, in temperate and
361 tropical areas. An example is provided in Figure 4. A great proportion of soils worldwide,
362 protected by permanent vegetation and possessing suitable moisture contents, comprise
363 large proportions of up to 60% macro-aggregates of both physical and biogenic types
364 (Velasquez et al., 2019).



365

366 *Figure 4: Relative proportions of biogenic, physicogenic macro-aggregates and non-macro-*
 367 *aggregated soil in different types of land use in the Eastern Plains of Colombia (Lavelle et*
 368 *al., 2014).*

369

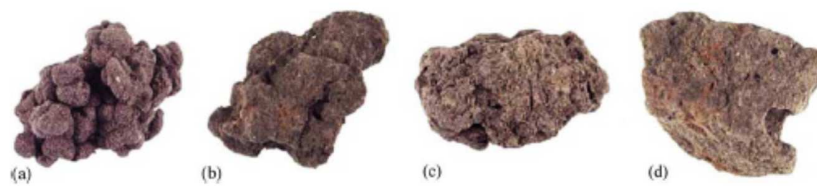
370 Physical aggregates are soil blocks produced by mechanical processes that create fissures in
 371 a continuous soil matrix (Boersma and Kooistra, 1994; Jongmans et al., 2001; Pulleman et
 372 al., 2005). They have angular blocky shapes with a dominance of sharp edges and plane
 373 surfaces. Particles within blocks are held together in a continuous matrix by organic and
 374 inorganic binding agents together with inter-particle binding due to Van der Waals forces
 375 (Hu et al., 2015). There is evidence that the same alternation of drying and rewetting
 376 events, that created these aggregates, may also activate the release of organic molecules,
 377 by microorganisms, that act as glues and consolidate these structures (Degens and
 378 Sparling, 1995; Cosentino et al., 2006). The addition of high molecular weight humic
 379 compounds may have similar effects (Piccolo et al., 1997; Yamaguchi et al., 2004). This set
 380 of aggregation processes when enhanced by physical compaction through use of tractors
 381 or cattle trampling in managed systems, tends to create very large clods and hard pans
 382 (Keen et al., 2013).

383

384 Biogenic aggregates are produced by organisms classified as ecosystem engineers for their
 385 ability to modify soil conditions through their physical activities (Blouin et al., 2013; Lavelle

386 et al., 2016). Ecosystem engineers produce a wide diversity of macro-aggregated
387 structures that differ significantly in their morphologies, chemical and biochemical
388 compositions (Decaëns et al., 2001; Mora et al., 2003; Velasquez et al., 2007b) (Figure 5).
389 Specific mineral compositions and organic matter contents and natures gives them rather
390 specific spectral signatures when illuminated with Near Infrared light (Hedde et al., 2005;
391 Dominguez-Haydar, 2018).

392



393

394 *Figure 5: Different kinds of soil macro-aggregates: a. biogenic (fresh earthworm cast); b.*
395 *biogenic (welded cast); c. intermediate (rounded aggregate); d. physicogenic (angular*
396 *blocky aggregate) (Photo: Pulleman et al., 2005).*

397

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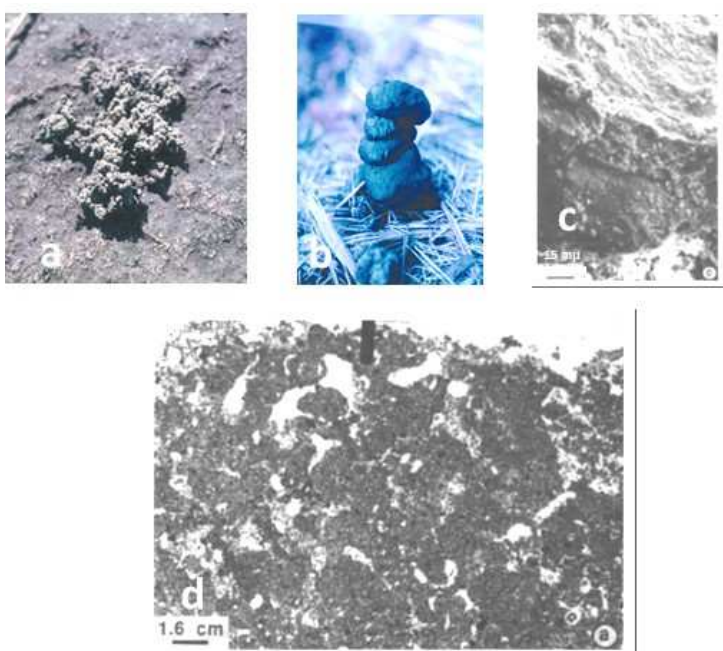
399 We recognize here four main categories which in turn comprise a large diversity of sub
400 categories.

401 *Fungal macro-aggregates* are created when fungal hyphae entangle organic debris and
402 mineral particles into stable aggregates that resist slaking and dispersion under the
403 mechanical stresses applied in classical tests. They are usually not separated in soils with a
404 permanent plant cover and are mostly seen in intensive cropping systems where
405 communities of other ecosystem engineers are depleted.

406 Most of the macro-aggregation described in soils of cropped fields and laboratory tests is
407 actually produced by this process (Tisdall and Oades, 1982; Plante and Mc Gill. 2002).
408 Mycorrhizal fungi are considered major producers of this type of aggregation (Rillig and
409 Mummey, 2006).

410 *Earthworms*_when present are major agents of soil bioturbation with widely different
411 effects depending on their ecological strategies (Bouché, 1977; Lavelle and Spain, 2001).
412 Epigeic earthworms live in the litter layers and are active composting agents that transform
413 litter into largely organic pellets. Anecic species live in deep, subvertical galleries

414 surrounded by zones of compacted soil that may behave as stable aggregated structures.
415 Their casts are usually relatively loose structures stabilized by high contents of 20 to 40%
416 on average (Judas, 1992) of little-decomposed particulate organic matter. Endogeic
417 earthworms live within the mineral soil horizons and feed on soil, with different
418 concentrations of organic matter depending on their specific – oligohumic, mesohumic or
419 polyhumic- adaptive strategies (Lavelle and Spain, 2001). They are the major producers of
420 biogenic macro-aggregates in many soils. They typically ingest from 1 to 10 and sometimes
421 up to 30 times their own weight of soil daily and total values of up to 1150 Mg dry soil ha⁻¹
422 have been measured, equivalent to a 10 cm thick soil layer (Lavelle, 1978). Their casts are
423 either highly compacted structures, with bulk densities as high as 1.8 to 2.0 Mg m⁻³
424 (Blanchart et al., 1993), or loose structures, easily disaggregated, produced by the endogeic
425 decomposing species (Blanchart et al., 1997).
426



427
428 *Figure 6: Loose (Chuniodrillus zieleae) (a) and compact (Reginaldia omodeoi) (b) earthworm*
429 *casts in African savanna (Lamto, Ivory Coast). (Photos P. Lavelle). Right: (c) Fracture of a*
430 *surface cast of R. omodeoi observed with SEM. Observe the cortex made of fine particles*
431 *that gives the surface of the cast a smooth and close aspect (Blanchart et al., 1993).*
432 *(d) Thin section in the 0-10 cm layer of a soil from a humid savanna (Lamto, Ivory Coast)*
433 *showing accumulation of globular casts mainly produced by the earthworm Reginaldia*
434 *omodeoi (Blanchart et al., 1997).*

435

436 The destruction and reorganization of aggregates may actually be a product of earthworm
437 activity itself in some soils.

438

439 *Social insect structures.* Termites and ants may be active producers of soil macro-
440 aggregates. Their bioturbation of several Mg ha⁻¹ year⁻¹ is the result of a mixture of digging,
441 building and casting activities (Lobry de Bruyn & Conacher 1990; Folgarait, 1998; Jouquet et
442 al., 2011). Aggregates formed that way vary from very loose deposits and faeces to very
443 compact tunnel-shaped aggregates or complex nest structures that may last years to
444 decades and even more (Rajagopal et al., 1982; Bonell et al., 1986; Mermut et al., 1994;
445 Humphreys, 1994; Gorosito et al., 2005; Korb, 2011; Erens et al., 2015).

446 Maybe even more remarkable is the formation by humivorous termites of structures
447 identified as pseudo-sand aggregates that end up comprising the entire volume of some
448 tropical ferralsols (Wielemaker, 1984, Eschenbrenner, 1986; Balbino et al., 2002; Reatto et
449 al., 2009; Millogo et al., 2011).

450

451 *Root aggregates* are structures that adhere to the roots. They are formed through five
452 different processes: local compaction of soil, water regime alteration, rhizodeposition of
453 gluing materials, decomposition of root material, and entanglement of soil particles by fine
454 (0.2 to 1 mm in diameter) roots (Monroe and Kladvko, 1987; Miller and Jastrow, 1990;
455 Morel et al., 1991; Materechera et al., 1992; Dorioz et al. 1993; Degens et al., 1994; Alami
456 et al. 2000, Czarnes et al. 2000, Gale et al. 2000, Feeney et al. 2006; Demenois et al., 2018).
457 An estimated 20% of plant photosynthesis is directly released at root tips with strong
458 biological effects and induced aggregation (Miller and Jastrow, 1990; Lavelle and Spain,
459 2001). Macro-aggregation by root activities may be a rather fast process. In a five-week
460 laboratory experiment, *Trifolium pratense* plants produced an average of 217.1 g and
461 *Plantago lanceolata*, 142.1 g of macro-aggregates in pots that contained 800 g of dry soil
462 moistened to field capacity (Zangerlé et al., 2011).

463

464 Mixed structures. Although some spectacular structures are produced by well-identified
465 single actors in nature or laboratory experiments, aggregation seems frequently to be a
466 cooperative process that involves different kinds of organisms, especially microorganisms.
467 There is also evidence that fine roots often colonize fresh earthworm casts and thus
468 possibly add their aggregative effects to those of the earthworm (Decaëns et al., 1999;
469 Zangerlé et al., 2011; Fonte et al. 2012). Fungal hyphae likely participate in the
470 consolidation of all sorts of other macroaggregates built by large ecosystem engineers.

471

472 Macro-aggregate specific identity and age

473 For a finer identification of physicogenic and biogenic macroinvertebrate or root macro-
474 aggregates, Near Infrared Spectrometry (NIRS) has proven to be a very efficient and
475 practical tool (Hedde et al., 2005). NIRS is a non-destructive method that reflects the
476 texture and amount and quality of organic matter contained in a soil sample. For each
477 sample, NIRS provides a spectrum that can be divided into separate ranges of wave length
478 longitudes (Velasquez et al., 2007b). Manually separated biogenic, physicogenic and non-
479 macro-aggregated aggregates exhibit significant differences (Dominguez-Haydar et al.,
480 2018). The same method perfectly discriminated structures produced by different macro
481 invertebrates (Hedde et al., 2005). Rather small samples of a few cg can be analysed
482 separately. It is therefore possible to analyse individually all the macro-aggregates from a
483 sample of a standard 10 x 10 x 10 cm size sample and group aggregates with similar
484 spectral signatures into homogeneous categories. Using this method, Zangerlé et al. (2016)
485 were able to separate eight categories of macro-aggregates from a forest soil in
486 Luxemburg. They further identified the earthworm species that had produced the structure
487 by comparing the spectral signatures with a bank of signatures established under
488 laboratory conditions. In another experiment, the same authors observed changes in the
489 spectral signature of casts as they aged (Zangerlé et al., 2014) showing potential of this
490 method to identify different phases in the stabilization, ageing and disaggregation process
491 of aggregates. Alternatively, enzymatic activities, microbial communities PLFA fingerprints
492 or physical and chemical variables have been shown to discriminate among biogenic

493 structures of different origins (Decaëns et al., 2001; Mora et al., 2003; Hedde et al., 2005;
494 Jouquet et al., 2013).

495

496 *3.3. Assessing the production and turnover of aggregates*

497

498 Our literature survey has confirmed that very few studies have been devoted to aggregate
499 production and turnover in natural or managed systems.

500

501 Field reaggregation or disaggregation tests

502 A simple way to approach the dynamics of aggregation can be obtained by applying an in-
503 situ re-aggregation or disaggregation test as done by Blanchart (1992), Barros et al. (2001
504 and Gorosito (2007()). Blocks of soil from 10 x 10 x 10 cm to 25 x 25 x 30 cm depending on
505 local conditions are taken in the field and a diagnosis of macro-aggregation is performed
506 using the methodology proposed in section 3.1. Soil is then crushed and passed through a
507 sieve with a 1 mm mesh size and taken back to fill the hole from which it had been
508 excavated and reaggregation is monitored. The unit is covered with some litter taken from
509 the surroundings and/or protected with a mesh to prevent the direct impact of rainfall that
510 would create physicogenic macro-aggregates. Different sizes of mesh may be used to allow
511 invertebrates and roots of different sizes to enter the experimental unit. Under these
512 conditions, ecosystem engineers from the surrounding soil and natural physical processes
513 will progressively form aggregates from the non-macro-aggregated soil. Experimental units
514 are excavated at regular time intervals to follow the restoration of the macro-aggregated
515 structure. In the experiment conducted by Blanchart (1992), the average percentage of
516 macro-aggregates > 2mm was 12.9% when macroinvertebrates were not allowed to enter
517 the unit, 49.9% when the mesh size allowed them to recolonize and 60.6% when the units
518 had been inoculated with endogeic earthworms. The dynamics of disaggregation can also
519 be observed putting the intact soil block, after fauna has been eliminated by a temporary
520 drowning, in a net that will not allow roots and invertebrates to come in (Blanchart et al.,
521 1997).

522 In some sites, macro-aggregate production can be measured using direct methodologies.
523 Production of surface and subterranean casts by earthworms, root macro-aggregates and
524 aggregated soil in the nest structures of termites and ants has been measured by ecologists
525 in a range of laboratory and field situations (Lavelle, 1978; Lobry de Bruyn et al., 1990;
526 Jouquet et al., 2013; Lavelle and Spain, 2001; Zangerlé et al., 2011) or simulated with
527 mechanistic models (Martin and Lavelle, 1992). Data are still scarce because these
528 measurements that require highly specific biological expertise are generally difficult and
529 time consuming, especially when measuring structures produced in the soil matrix.

530

531 Spectral analysis of individual macro-aggregates

532 Macro-aggregates of biogenic root or invertebrate origin have a specific spectral signature
533 that mostly reflect specific quality and concentrations of organic elements and texture
534 (Hedde et al., 2005; Velasquez et al., 2007a; Zhang et al., 2009; Zangerlé et al., 2011).
535 These specific signatures seem to progressively converge towards a common “bulk soil”
536 signature as the structure ages. In a laboratory study conducted with the endogeic species
537 *Aporrectodea caliginosa*, spectral signature of casts changed first rapidly, in the first 2 days
538 after deposition and then slowly until day 45 to 60 when it was difficult to separate it from
539 the bulk soil signature. This method allowed to separate casts aged less than 60 days and
540 get an estimate of macro-aggregates of a given category during a 2-month period.
541 (Zangerlé et al., 2016).

542

543 Turnover time in steady state situations

544 In a steady state situation, the amount of new structures created is expected to be
545 compensated by the destruction of an equal amount. Based on reaggregation experiments
546 conducted in natural environment, Blanchart (1992) was able to evaluate at 20 months and
547 28 months, in grass and shrub savannas respectively, the average residence time of casts of
548 the earthworm *Reginaldia omodeoi* in a savanna of Ivory Coast. In this case,
549 complementary studies have shown that macro-aggregated structures created by this

550 earthworm are eaten by another earthworm species from the Eudrilidae family that
551 transform these highly compact casts into fragile erodible soil pellets (Blanchart et al.,
552 1997). Very fast transformations of the soil structure have been observed with this method.
553 In an experiment conducted in Amazonia, Barros et al, (2001) exchanged undisturbed soil
554 blocks from a pasture and the natural forest to the other site. After one year, the heavily
555 compacted soil of the pasture had recovered a macro-porosity close to that of the forest,
556 while forest blocks inoculated in the pasture has almost attained the levels of compaction
557 observed in this pasture. A similar experiment allowed Gorosito (200) to demonstrate that
558 soil blocks from rice fields derived from a natural savanna were rapidly colonized, with
559 similar abundances and diversities after one year and even higher values after 2 years.
560 Similar approaches developed with plants and other producers of biogenic aggregates
561 might provide some estimates on the life duration of these structures. Further studies will
562 then be required to identify the predominant disruption process and the fate of
563 microaggregates that they contained.

564

565 *4 C cycling and soil aggregation*

566

567 Once recognized and measured the different aggregate pools in soil, the effect of soil
568 aggregation dynamics on C cycling can be assessed using a simple conceptual framework
569 (Figure 3). Assessing the effect of each recognized pool on soil C cycle first requires an
570 evaluation of the energy cost (as mineralized C) of creating these macro-aggregates, if
571 relevant. Then we need a precise knowledge of the amount and quality of the organic
572 matter contained in this pool and an estimate of the persistence and general dynamics of
573 the specific aggregate pool. In addition, one must have some ideas on the processes that
574 lead to their disruption and transfer to the non-macro-aggregated pool or to another pool.

575

576 Soil C in aggregates and aggregation dynamics

577 Analysis of C contents separated among particulate organic matter (POM) and MAOM
578 fraction associated to the soil mineral fraction will be applied to samples from the different
579 recognized aggregate pools. This will allow measuring stocks of C associated to the

580 different pools. A number of studies has shown strong effects of plant cover and soil
581 management on these stocks and their temporal variations (Dexter et al., 1999; Conant et
582 al., 2001; Post et al., 2000; Martens, 2000; Zhang et al., 2013; 2016).

583 We hypothesize that transformations of particulate and mineral-associated organic matter
584 are linked to those of the aggregated or non-aggregated mineral pools that comprise them.
585 Dead fine and coarse root material and root exudates are transferred to the root biogenic
586 macro-aggregated structures (CBM roots) through rhizospheric activities. Organic debris of
587 root origin occasionally ingested by invertebrates will be further included in their faecal
588 pellets as earthworm casts or as organic macro-aggregates of rhizophagous coleoptera
589 larvae in other fractions of the CBM pool. Organic matter deposited in the leaf litter layer,
590 the other source of organic materials, is first transformed by comminution and natural
591 composting processes and progressively incorporated to the soil by digestion and
592 bioturbation processes associated with macroinvertebrate feeding activities and leaching of
593 dissolved organic matter. The decomposition rate of this organic matter is influenced by
594 the same processes that lead to its incorporation in the aggregates, gut transit or burial
595 below earthworm casts and insect deposits at the soil surface.

596

597 Energy cost of macro-aggregate production

598 As indicated before, the formation of certain biogenic macroaggregates has a significant
599 cost in energy and C emission. This C loss may be evaluated by comparing C contents of the
600 non-macroaggregated material originally used with the macroaggregates produced, or
601 measuring the respiratory costs associated with the mechanical activities associated to
602 their formation (Lavelle, 1978).

603

604 Carbon emission from the aggregated and non-macro-aggregated pools

605 A large number of studies have compared the respiration activity of aggregates of different
606 size fractions and in different conditions of soil management (Dexter et al., 1999; Ashman
607 et al., 2003; Zhang et al., 2013; 2016). Carbon from each pool is mineralized at different

608 rates. For example, Martin (1991) showed that C mineralization proceeded at a much lower
609 rate in casts of *Reginaldia omodeoi* than in the non-ingested soil sieved at 2mm. Digestion
610 of the soil prior to cast release had decreased the C content of the soil by 9%, but
611 mineralization inside the very compact cast had decreased microbial activity to such a low
612 value that the non-digested soil and the cast had the same C contents after 100 days. With
613 each day past this limit, the difference in C contents between macro-aggregated and non-
614 macro-aggregated soil would increase. Where casts may persist from 20 to 28 months, the
615 ability of this species and type of biogenic aggregate to conserve C may be very important.
616 The expected 'protection' of C from mineralization however will likely depend on conditions
617 created within the structure: aeration, temperature and moisture conditions,
618 stoichiometric and other chemical environment conditions.

619 The major water-soluble organic sources, root exudates, earthworm intestinal mucus or
620 termite saliva that represent inputs of several Mg C per ha per year are mixed with the
621 mineral soil and soon become part of the macro-aggregated soil fraction, in the forms of
622 earthworm casts, root macro-aggregates or termite constructions.

623 In the absence of invertebrate ecosystem engineers, leaf litter organic matter stays at the
624 soil surface and the production of organo-mineral macro-aggregates is limited to root
625 aggregate production. Water soluble organic matter leached from the litter layer may well
626 circulate among macro-aggregated fractions as part of the soil drainage process and
627 stimulate microbial decomposing activities creating priming effects (Fontaine et al., 2007).
628 It should, however, not have a significant effect since it represents a rather limited flow as
629 compared to other components of organic matter inputs (Lavelle and Spain, 2001; Jimenez
630 and Lal, 2006). It is also expected to be rapidly flocculated in the presence of clay minerals
631 (Toutain, 1981) or consumed upon entering the soil matrix and does not enter easily inside
632 compact aggregates

633 Carbon in the non-macro-aggregated soil pool (C_{NMS}) may have been released from
634 disaggregated biogenic or physical aggregates or be generated by flocculation or
635 condensation processes of water-soluble organic matter occurring in the interaggregate

636 space. Carbon of the physicogenic macro-aggregate pool (C_{PM}) may have been contained in
637 the non-aggregated pool before it was transformed into physical aggregates.

638

639 5 Discussion

640

641 Our literature review confirmed that biological processes are severely undermined in
642 aggregate studies was confirmed: only 11.5% of the papers considered microbial
643 components, and 4% roots and invertebrate activities. This is clearly the result of restricted
644 disciplinary focus where a holistic view is necessary (Lavelle et al., 2016; Briones, 2018).
645 Five other important gaps, addressed below, appeared that are susceptible to hinder a
646 global and practical understanding of processes at hand and ways to enhance their benefits
647 in terms of ecosystem services. The approach that we propose to attain this goal is based
648 on a number of assumptions, conceptual simplifications and the choice of technical options
649 that often coincide with these gaps.

650

651 Definition and classification of aggregates: The need for a comprehensive separation
652 technique that combines viewing and isolating approaches.

653 Soil macroaggregates may be seen in very different ways by scientists depending on the
654 discipline they belong to. For soil ecologists, technicians and farmers, they often are visible
655 and easily recognizable structures created by roots and invertebrate ecosystem engineers
656 (Lavelle et al., 2006; Blouin et al., 2013; Jouquet et al., 2016). A severe drawback of using
657 stress resistance of aggregates as a way to isolate them is that part of the resistance is
658 provided by chemical and biological binding effects associated to the soil type, and not to
659 the macro-aggregation process itself. On the other hand, a direct relationship between
660 stabilization and conservation of C in soil conditions has not been proven to our knowledge.
661 The manual separation technique that we propose is a combination of viewing and
662 isolation techniques. This technique has proven very efficient at showing scientists,
663 students and farmers the importance and vulnerability of the macro aggregation in soils.
664 Synthetic indicators made with data provided with this method are always linked with

665 other physical, chemical or biological attributes of soil fertility and ecosystem services
666 provisioning (Velasquez et al., 2007b; Lavelle et al., 2014; Grimaldi et al., 2014; Velasquez
667 ad Lavelle, 2019). When the objective is to show the importance of the macro aggregation
668 process to students or farmers and differential effects of soil management options, no
669 specific training is required since trainees will separate structures the same way, whatever
670 it is, in different soils and perceive differences. Efforts should be done however, to better
671 standardize this technique (Jouquet et al., 2009). Clear recommendations should be made
672 on how to properly disrupt the soil matrix according to natural breaking surfaces, in
673 different conditions of soil texture and plant root densities. Separation of root and other
674 biogenic aggregates may require specific actions depending on their sizes and structures.
675 Soil texture - especially when clayey- or effects of mismanagement -when soils are highly
676 compacted- may complicate this technique in some situations. An important issue is the
677 size of the elements that have been identified as macro-aggregates. When felt important,
678 smaller sieves could be used to isolate fractions down to 1, or even 0.25 mm. In this case,
679 the observation of subsamples with a stereo microscope may provide the accuracy
680 required by specific scientific studies (Topoliantz et al., 2000).

681

682 Macro vs. microaggregates. Can microaggregates be independent of macro-aggregates?
683 And to what extent?

684 The idea that microaggregates are formed inside macro-aggregates (Six et al. 2000) offers a
685 welcome simplification in our approach. It is also in accordance with the self-organized soil
686 model that proposes a hierarchical organization of soil, with successive functional units
687 nested in each other as their size increases (Lavelle et al., 2016). While this view of soil
688 organization is widely acknowledged and demonstrated by an important number of studies
689 (Six et al., 2000; Bossuyt et al., 2004; Fonte et al., 2012), a few questions remain. First
690 microaggregates are not a homogeneous category (Tötsche et al, 2018) although, there is
691 some expectation that microaggregates have compositions derived from that of
692 macroaggregates, although with generally less C and lower C:N ratio (Blanchart et al.,
693 2000). Maybe more important is knowing what happens to microaggregates when

694 macroaggregates get disrupted. In the model of aggregate dynamics proposed by Marquez
695 et al. (2018), microaggregates may be either disrupted when the macro-aggregate that
696 comprise them is disrupted or be part of a transient fractions that is further reincorporated
697 into macro-aggregates.

698

699 Identify aggregate origins to understand biological or other processes that determine their
700 creation and further dynamics.

701 The very low proportion of articles that consider root or invertebrate generation of macro-
702 aggregates points at a very important gap. Specificities of composition, structure and
703 microbial communities at species level of these macro-aggregates are very important
704 determinants of their further stability and temporal dynamics (Hedde et al., 2005; Mora et
705 al., 2003; Jouquet et al., 2013). NIRS has been showed to offer a cheap and efficient way to
706 solve the problem. However, NIR spectral signatures have also proved to be unstable in
707 ageing earthworm casts (Zangerlé et al., 2014). Changes in spectral signature probably
708 reflect the rapid changes of microbial biomass and mineral N contents observed in freshly
709 deposited earthworm casts (Lavelle et al., 1992). The Intriguing observation that casts aged
710 >45 days have a signature similar to the bulk soil should be further investigated. Does this
711 mean that the surrounding soil was actually mostly comprised of aged earthworm casts of
712 the species considered? Or can we think of an alternative hypothesis? Fresh macro-
713 aggregates are hotspots of microbial activity where some microbial species are enhanced,
714 not the whole soil community. Would the specific signature observed in freshly created
715 structures reflect important transient biomass of these components? And signature
716 observed later on an indication that these populations have decreased to their initial
717 abundance in the bulk soil? Comparable observations made by Blackwood and Paul (2003)
718 show the importance of this question.

719

720

721

722

723 Interactions among physicogenic and biogenic agents in soil macro-aggregation dynamics

724 In a finite soil volume, formation of new macro-aggregates in a steady state formation has
725 to be done at expenses of other pools of aggregated or non-aggregated soil. Stable macro-
726 aggregates produced by a given set of invertebrates or roots can be destroyed by other
727 invertebrates that may use them as food, or roots and invertebrates that just need to make
728 their way through the soil to grow or develop their porous domains. Organisms may
729 cooperate in forming macro-aggregates. This is the case for example for earthworms and
730 roots, although cooperation may well be specific (Zangerlé, et al., 2011). The equilibrium
731 among ecosystem engineers with opposite compacting or decompacting effects may be a
732 critical element when considering soil management options (Blanchart et al., 1997; Chauvel
733 et al., 1999). Research on this topic is virtually absent.

734

735 C loss and conservation associated to aggregation

736 While soil aggregation is largely associated with C accumulation in soils, detailed underlying
737 mechanisms are far from being completely understood. The option of our model,
738 considering C cycling as a discrete process split among different aggregate pools of
739 different origins with different histories probably deserves improved theoretical and
740 experimental foundations. In surface soil layers where biological activity is concentrated,
741 aggregation seems to be the best option for limiting C mineralization. A better
742 understanding and classification of biological aggregation processes would probably help.
743 The overall effects of these aggregation processes on C cycling might well differ along a
744 continuum from short term fungal hyphae particle entanglement observed in poorly
745 aggregated agricultural soils to potentially long-lived earthworm casts stabilized by a drying
746 event or aggregates associated with social insect nests. In both extreme cases, respiration
747 of the organisms responsible for the creation of aggregates have very different energy
748 costs that should be incorporated in models. One can hypothesize that in steady state
749 conditions, the cost of creating aggregates is compensated by their protection effect on soil
750 organic matter (Lavelle and Spain, 2001; Lubbers et al., 2017). Disaggregation of soils

751 associated to intensive cropping practices may be explained by increased microbial
752 mineralization in conditions where macro-aggregation by ecosystem engineers is deficient.
753 In other cases, excessive activity of invasive ecosystem engineers, like European earthworm
754 species in northern America forests, may well increase soil aggregation while soil C stocks
755 decrease. Bioturbation activities then exceed the effect of physical protection in
756 aggregates (Bohlen et al., 2004).

757 With soil depth, oxygen concentration naturally decreases and the mere rarefaction of
758 biological activity is thought to favor C conservation. Mechanisms and conditions that allow
759 migration of C in deep layers also require better understanding.

760

761 6 Conclusion

762

763 Synthesis of knowledges generated in different disciplinary fields led us to propose an
764 alternative approach to evaluate the process of aggregate formation and its contribution to
765 the conservation and accumulation of organic matter in soils. The methodology proposed is
766 based on relatively simple and low-cost techniques that should be accessible to a large
767 number of scientists, technicians and farmers. This condition is important to develop multi-
768 functional agricultural practices that contribute to restore soil- based ecosystem services
769 and especially soil critical contribution to the mitigation of global warming.

770 Explicitly considering biological mechanisms that determine soil aggregation will allow
771 harnessing this process to ecosystem restoration practices and sustainable management
772 options. In soils considered as self-organized systems, aggregates are constructed
773 structures that have positive feedbacks on the communities that produced them (Lavelle et
774 al., 2016; Bedano et al., 2019). Aggregation is part of the “potential” of the ecosystem as
775 defined by Holling (2000), a capital that varies along adaptive cycles and that determines
776 ecosystem evolution. In situ soil reaggregation tests, that indirectly evaluate the ability of
777 organisms to collectively organize and improve their habitat, might well appear as a simple
778 way to measure such an important attribute. This evaluation of potential combined with an
779 assessment of the connectance, mostly linked to local diversity and abundance of plant and

780 invertebrate ecosystem engineer communities, should allow progressing in the base line
781 evaluation of ecosystems before initiating restoration practices.

782

783

784 7 References

785

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